

AN EARLY CRETACEOUS ANGIOSPERM FOSSIL OF POSSIBLE SIGNIFICANCE IN ROSID FLORAL DIVERSIFICATION

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ABSTRACT

Lachnociona terriae gen. & sp. nov. is described from an Early Cretaceous flower preserved in Burmese amber. *Lachnociona* is represented by a small, hirsute, functionally pistillate flower with 5 strongly recurved perianth parts, 10 staminodial filaments, and a 5-carpellate pistil with 5 stout, erect, connivent or connate styles, their sharply acute, recurved tips presumably with decurrent ventral stigmas. The gynoecium is densely lanate-hirsute. Three of the filaments show thin pieces of vestigial anther tissue at their tips. The perianth is interpreted as a calyx, with the corolla absent. Possible relationships are discussed, focusing on the families Brunelliaceae and Cunoniaceae (order Oxalidales), and on selected examples from 2 other rosid orders plus Saxifragales.

RESUMEN

Se describe **Lachnociona terriae** gen. & sp. nov. a partir de una flor conservada en ámbar del Cretácico temprano de Birmania. *Lachnociona* está representada por una flor pequeña, hirsuta, funcionalmente pistilada con perianto de 5 partes fuertemente recurvadas, 10 filamentos estaminodiales, y un pistilo 5-carpelado con 5 estilos fuertes, erectos, conniventes o connatos, con los extremos muy agudos y recurvados, presumiblemente con estigmas ventrales decurrentes. El ginoecio es densamente lanoso-hirsuto. Tres de los filamentos muestran piezas finas de tejido vestigial de la antera en sus extremos. El perianto se interpreta como un cáliz, con la corola ausente. Se discuten las posibles relaciones, centrándonos en las familias Brunelliaceae y Cunoniaceae (orden Oxalidales), y en ejemplos selectos de otros dos órdenes de rósidas y de Saxifragales.

INTRODUCTION

Burmese amber is first mentioned in works dating from AD 100, when an amber trade route was established between that country and China. From AD 100 until 1936, the Burmese amber mines supplied amber for jewelry and fossils. Social upheavals closed the mines for 63 years, but in 1999, extraction procedures began anew. The fossil was derived from a mine first excavated in 2001, in the Hukawng Valley, southwest of Maingkhwan in the state of Kachin (26°20'N, 96°36'E) in Burma (Myanmar). This new amber site, known as the Noiye Bum 2001 Summit Site, was assigned to the Upper Albian of the Early Cretaceous on the basis of paleontological evidence (Cruickshank & Ko 2003), placing the age at 97 to 110 mya. Nuclear magnetic resonance (NMR) spectra and the presence of araucarioid wood fibers in amber samples from the Noiye Bum 2001 Summit Site indicate an araucarian (possibly *Agathis*) tree source for the amber (Poinar et al. 2007).

Within the past few years, amber from this area has yielded a wealth of arthropod and plant remains (Poinar et al. 2005). While insects dominate, some very interesting angiosperm fossils have been recovered up to now, including flowers with possible affinities to the families Monimiaceae (Poinar & Chambers 2005) and Cornaceae (Poinar et al. 2007), as well as two early bambusoid grasses (Poinar 2004). In the present paper, we describe an additional flower from the same location, with similarities to fossil and extant members of eurosid orders Oxalidales, Cucurbitales, Sapindales, and eudicot order Saxifragales.

MATERIALS AND METHODS

An entire, well-preserved female flower with staminodes (accession # ab-294) is embedded in a round piece

of amber with a diameter of 40 mm and a thickness of 5 mm. Examination and photographs were made with a Nikon stereoscopic microscope SMZ-10 R at 80 \times and a Nikon Optiphot microscope at 800 \times .

DESCRIPTION

Lachnociona G.O.Poinar, K.L. Chambers & R. Buckley, gen. nov. TYPE SPECIES: *Lachnociona terriae* G.O. Poinar, K.L. Chambers & R. Buckley, sp. nov.

Diagnosis.—Flowers small, pedicellate, unisexual, the type specimen functionally pistillate, 5-merous, actinomorphic, apparently apetalous; sepals 5, regular, separate, ovate-lanceolate, recurved, ciliate, lightly hirsutulous on both surfaces, venation obscure; staminodes 10, in 1 or 2 whorls, filaments conspicuous, slender and tapering, the tip retrorsely hooked in some, the fully preserved ones all non-functional, anthers absent or represented by thin vestigial tissue on 3 staminodes; gynoecium 5-carpellate, densely lanate-hirsute, ovary superior or perhaps half-inferior, it and the disc (if present) concealed by the pubescence, styles connivent or partly united, their tips sharply acute, recurved-divergent in the upper 1/4–1/3, the stigma probably decurrent ventrally; staminate flower and fruit unknown.

Lachnociona terriae G.O.Poinar, K.L. Chambers & R. Buckley, sp. nov. (**Figs. 1–4**). TYPE: MYANMAR (Burma): amber mine in the Hukawng Valley; SW of Maingkhwan in the state of Kachin (26°20'N, 96°36'E), northern Myanmar, 2001, *unknown amber miner s.n.* (HOLOTYPE: accession no. ab-294, Burmese amber, deposited in the collection of Deniz Erin of Istanbul, Turkey, 34744). Arrangements to study the type specimen can be made by contacting Ron Buckley at ronbuckley@fuse.net.

Description.—Flower length 5.6 mm; flower width 5 mm; sepal length 3.60 mm, width 1.8 mm; length of trichomes on sepals 0.25–0.36 mm; staminodes exerted, most broken or chewed off; length of remaining filaments 1.80–1.90 mm; length of vestigial anthers 0.11–0.88 mm; width of largest anther 0.20 mm; length of gynoecial column 3.30 mm; length of divergent upper lobes of style 1.20 mm; length of subtending bract on pedicel 1.10 mm; distance from base of bract to summit of hirsutulous pedicel 2.90 mm.

Etymology.—Genus name from the Greek “lachnos,” woolly hair, and “kion,” column, with reference to the projecting stylar portion of the gynoecium. Species named in honor of the collector, Mrs. Terri Millinoff.

DISCUSSION

The salient features of the fossil, as described above, are its unisexuality, apparent apetalous, 10 staminodes, densely pubescent, 5-carpellate gynoecium, stout stylar column, and acute, spreading stigmatic lobes. The most reasonable interpretation of the ovary is that it is either superior or, judging from the expanded distal region of the pedicel, half-inferior. The vestigial anther tissue on 3 of the filaments is noteworthy, suggesting unisexuality by abortion, hence derivation from hermaphrodite ancestors. In framing a hypothesis for the systematic position of *Lachnociona*, we have searched for present-day families which best fit the above group of traits, if reasonable assumptions are made about features not clearly visible in the fossil. Because of the thick covering of darkly pigmented hairs, microscopic study of this structure could not resolve the choice between fused or connivent styles. As well, the recurved perianth parts with dark coloration at their base prevented observation of any tiny, outer perianth parts beneath them, and we thus interpret the perianth as a calyx, with the corolla either lacking or deciduous.

Possible candidates have been identified as the closely associated families Brunelliaceae and Cunoniaceae (Oxalidales) (APG II 2003; Stevens 2001 onwards; Soltis et al. 2005), both groups occurring mainly in the Southern Hemisphere with representatives, in the latter case, in the Australian-Southeast Asian region. We interpret the stout, densely hairy, darkly colored (in the fossil) columnar structure to be, all or in part, 5 connivent-appressed styles. The Late Cretaceous fossil *Platydiscus* (Schönenberger et al. 2001; Schönenberger & von Balthazar 2006; Friis et al. 2006) was included in our analysis, because of its initial association with Cunoniaceae. Also, *Anisophyllea* (Anisophylleaceae), of order Cucurbitales, and *Aphanopetalum* (Aphanopetalaceae), of order Saxifragales, came under consideration. *Eurycoma* (Simaroubaceae, order Sapindales) was added for a comparison involving a different interpretation of the perianth of the fossil.

Table 1 summarizes a comparison of floral traits of *Lachnociona* with four living members of Brunelliaceae and Cunoniaceae, together with *Platydiscus*, *Anisophyllea*, *Aphanopetalum* and *Eurycoma*. Brunelliaceae and

TABLE 1. Comparison of *Lachnociona* with fossil and recent Cunoniaceae (*Platydiscus*, *Spiraeanthemum*, *Pullea*, *Vesselowskyia*), Brunelliaceae (*Brunellia*), Anisophylleaceae (*Anisophyllea*), Aphanopetalaceae (*Aphanopetalum*), and Simarubaceae (*Eurycoma*).

	<i>Lachnociona</i>	<i>Platydiscus</i>	<i>Spiraeanthemum</i>	<i>Pullea</i>	
1. Pedicel present - +, absent - 0	+	+	+	+, 0	
2. Sepals free - +, connate* - 0	+	+	+, 0	+	
3. Sepal number	5	4	4(5)	5(6)	
4. Sepals spreading - +, upright - 0	+	+	0	+	
5. Petals absent - +, present - 0	+	0	+	+	
6. Flowers unisexual - +, bisexual - 0	+	0	+	+	
7. Stamen number	10	8	8(10)	10(12)	
8. Ovary superior - +, \pm , inferior - 0	+ or 0	0	+	0	
9. Ovary apocarpous - +, syncarpous - 0	+ or 0	0'	+''	0	
10. Carpel number	5	4	(2-3)4 or 5	2	
11. Styles united - +, separate - 0	+ or 0	0	0	0	
12. Style tips acute - +, capitate - 0	+	+°	0	+	
13. Stigma decurrent - +, terminal - 0	+?	+°	0	0	
14. Gynoecium hairy - +, glabrous - 0	+	+	+	+	
15. Free styles connivent - +, spreading - 0	+?	+°°	0(+)	0(+) ¹	
(genera continued)	<i>Vesselowskyia</i>	<i>Brunellia</i>	<i>Anisophyllea</i>	<i>Aphanopetalum</i>	<i>Eurycoma</i>
1.	+	+	0	+	+
2.	+	+	+	+	+(small)
3.	3(4)	(4)5(6)	(3)4(5)	4	5
4.	?	+ or 0	0	0	0
5.	+ or 0 ²	+	0	0(+, small)	+(large)
6.	+	+ (0)	+	0	+(0)
7.	6(8)	(8)10(12)	(6)8(10)	8	5 large
8.	+	+	0	0	+
9.	0	+	0	0	+
10.	2	(3-4)5(6)	(3)4(5)	4	5
11.	0	0	0	+	0 or + ³
12.	+	+	+	+	+
13.	+	+	+	0	+
14.	+	+	0	0	+
15.	0	0(+)	+	-	+

Footnotes: * - not counting basal fusion to pistil in 1/2 inferior ovaries; ' - synascidiate below, free above; '' - laterally connate at base; ° - style tips broken below tip, reconstructed as acute with ventral slit (implying decurrent stigma?); °° - spreading above in reconstruction, but connivent below in figs. 21, 34 in Schönerberger et al., 2001; ¹ - connivent when young, see Dickison 1975, fig. 15h; ² - female flowers have only sepals, Dickison 1989; ³ - separating in fruit.

References: Cuatrecasas 1970; Dickison 1975, 1989; Engler 1930a,b, 1931; Friis et al. 2006; Hermsen et al. 2006; Heywood 1978, p. 158; Hoogland 1979; Hufford & Dickison 1992; Kubitzki 2004, 2007; Matthews et al. 2001; Matthews & Endress 2004; Nooteboom 1962; Orozco Pardo 2002; Perry 1949; Schönerberger et al. 2001; Smith 1952, 1985; Takhtajan 1996.

Cunoniaceae, sometimes united into one family, have always been considered as closely related in traditional theories of angiosperm phylogeny (e.g., Engler 1930a, b; Thorne 1992; Cronquist 1981). The fossil is similar to *Brunellia* in being unisexual, apetalous, 10-stamened, and having a 5-carpelled, pubescent gynoecium with acute style tips whose stigmatic surface is probably ventral and decurrent. *Brunellia* is apocarpous, the carpels at most being immersed in the disc (Orozco Pardo 2002; Kubitzki 2004). Its separate styles may be vertical in early flower (Cuatrecasas 1970; Kubitzki 2004), with recurved tips. In Cunoniaceae, the carpel number is usually 2 and the stigmas, except for *Vesselowskyia*, are terminal and often capitate (Bradford et al. 2004). However, higher carpel numbers are known, e.g., in *Pullea*, *Aistopetalum*, *Spiraeanthemum*, and

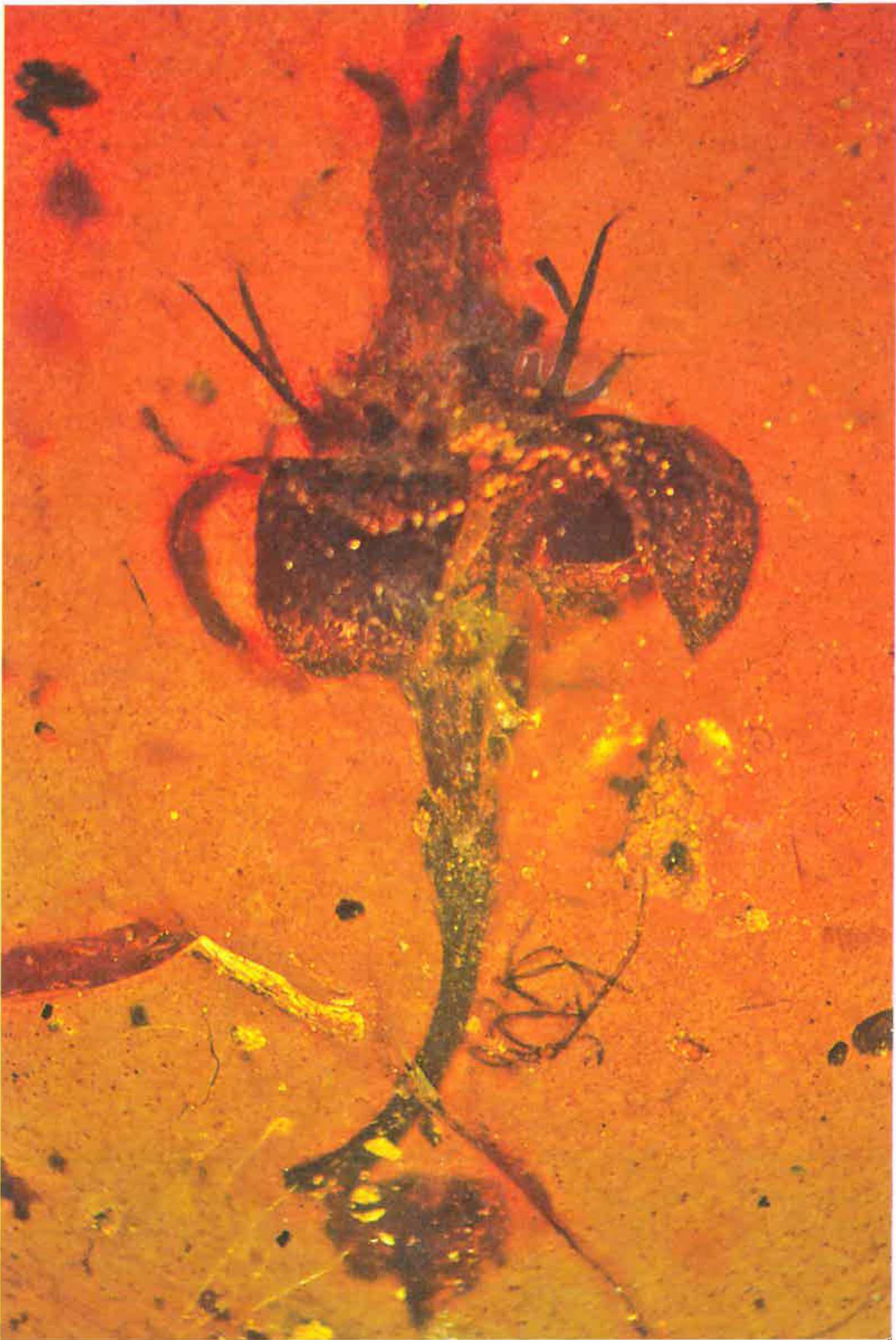
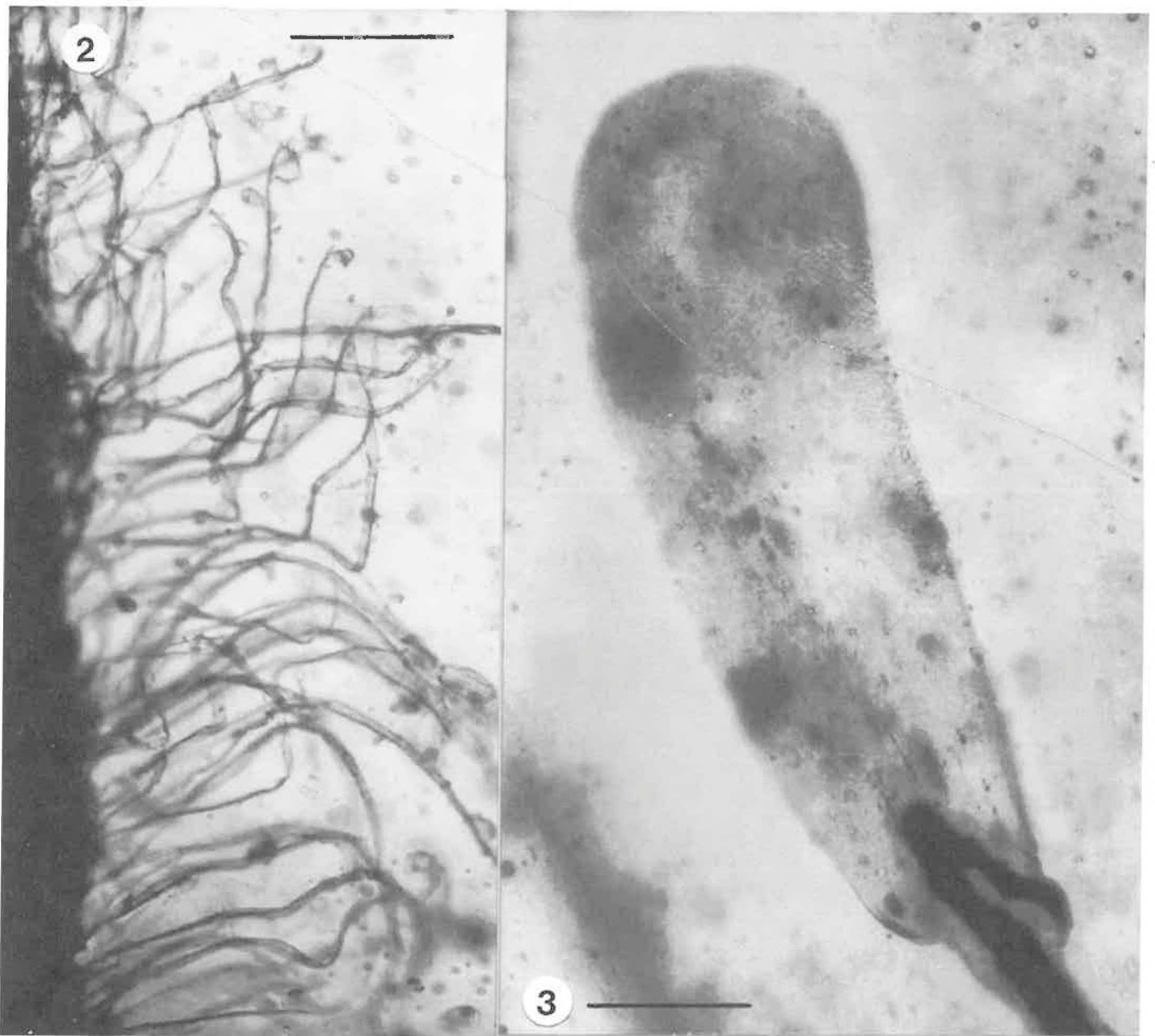


FIG. 1. Flower of *Lachnociona terriae* in Burmese amber. Holotype specimen. Scale bar = 1.43 mm.

Acsmithia, the latter two genera comprising a possible morphological link with Brunelliaceae (Orozco Pardo 2002; but see Bradford & Barnes, 2001, for DNA evidence supporting their inclusion in Cunoniaceae). Genera of Cunoniaceae with unisexual flowers include *Spiraeanthemum*, *Pancheria*, and *Vesselowskya*, and the latter genus is unique in the family in showing a ventrally decurrent stigma like that of *Brunellia* (Dickison 1989, fig. 4.3; Hufford & Dickison 1992) and putatively like that of *Lachnociona*. That the ovary of the fossil might be half or more inferior (judging from the expanded apex of the floral pedicel) was mentioned above; in this, it would resemble *Schizomeria* (Matthews & Endress 2002) and *Pullea* (Dickison 1975) and differ from *Spiraeanthemum* and *Vesselowskya*. The styles may be erect and partially connivent in some Cunoniaceae (at



FIGS. 2–3. Flower of *Lachnociona terriae* in Burmese amber. 2. Long trichomes on surface of sepals. Scale bar = 126 μm . 3. Transparent vestigial anther. Note reflexed tip of filament. Scale bar = 123 μm .

least in early flower), as illustrated for *Pullea* and *Acsmithia* by Dickison (1975, fig. 15h, and 1989, fig. 4.2B, respectively) and Hoogland (1979, fig. 1). Of the above-mentioned genera, petals are absent in *Brunellia*, *Spiraeanthemum*, *Acsmithia*, *Pullea*, and (in pistillate flowers) *Vesselowskya* (Dickison 1989). None of the modern genera listed have styles pubescent nearly to the tip like *Lachnociona*.

Aphanopetalum (Aphanopetalaceae) is included in Table 1; it has a 4-carpelled gynoecium with half-inferior ovary, and a stout stylar column with spreading, terminally-stigmatic tips (Dickison 1975, fig. 1a). Dickison (op. cit.) shows a median longitudinal section of a flower nearing anthesis; its thick style of 4 fused carpels with spreading, bluntly pointed tips very much resembles the stout (but more acutely tipped) gynoecium of *Lachnociona*. Significant differences are evident, however, in the androecium of 8 large, fertile, nearly sessile anthers of *Aphanopetalum*, the 4-merous calyx, and the presence of 4 poorly developed petals. The flowers of *Aphanopetalum* are glabrous, as well. This genus has an interesting taxonomic history, having been placed originally in Cunoniaceae (Engler 1930b; Dickison 1975; Hufford & Dickison 1992), but it was found by Bradford and Barnes (2001) to be better placed in or near Saxifragaceae, according to their analysis of the *TrnL-F* intron of the chloroplast tRNA-Leu gene. Based on the morphological work of

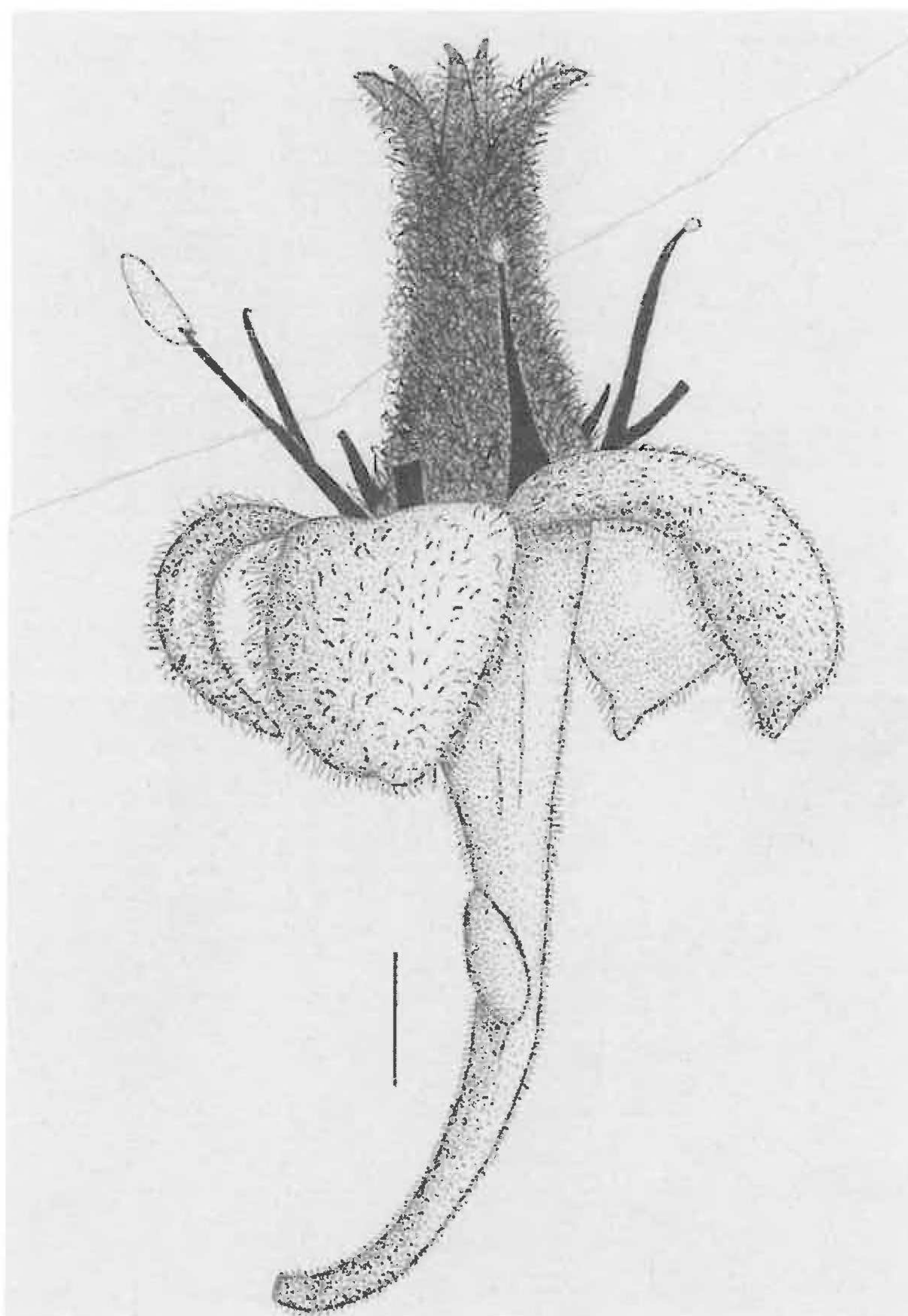


FIG. 4. Drawing of flower of *Lachnociona terriae* in Burmese amber. Scale bar = 1 mm.

Dickison et al. (1994) and the molecular phylogenetic studies by Fishbein et al. (2001) and Hermsen et al. (2006), *Aphanopetalum* is now placed as a monotypic family of the order Saxifragales (Stevens 2001 onwards; Soltis et al. 2005).

Platydiscus is a well-studied charcoalfied Late Cretaceous fossil flower from sand and clay sediments of the Kristianstad Basin in Scandia, Sweden (Schönenberger et al. 2001, see drawing of a reconstruction in Friis et al. 2006). The perianth is 4-merous, with small, densely glandular petals and spreading sepals, stamens are 8 and fertile, and the gynoecium of 4 carpels has a half-inferior ovary and connivent, erect styles. The spreading stylar tips are reconstructed as acute with a ventral slit; the stigmatic region is not described but may well have followed the slit as, e.g., in *Brunellia* and *Vesselowskya* (our suggestion, not the authors'). The connivent styles, with broken off tips, are well illustrated by Schönenberger et al. (2001, figs 34 and 40). Features of the gynoecium of this fossil, as illustrated and reconstructed, are thus quite reminiscent of *Lachnociona* as we visualize it. Differences between our fossil and *Platydiscus* are that the latter is 4-merous throughout, bisexual, and petaliferous. Its age, given as Late Santonian–Early Campanian, is approximately 20 my younger than that of the fossil reported here from the Early Cretaceous.

The possible phylogenetic relationship of *Platydiscus* to Cunoniaceae and Anisophylleaceae, and that of the latter two groups to each other, was discussed by Matthews et al. (2001), who pointed out the anomalous position of the latter family in the order Cucurbitales (see also Tobe & Raven 1988). However, this ordinal assignment is well borne out by recent molecular studies (Schwarzbach & Ricklefs 2000; Zhang et al. 2006).

The flowers of *Anisophyllea* are similar in many ways to those of Cunoniaceae and *Platydiscus*, as cited in detail by Matthews et al. (2001). Like *Lachnociona*, *Anisophyllea* is unisexual, with two whorls of stamens, separate acute styles, and stigmas decurrent ventrally (Matthews et al. 2001; Matthews & Endress 2004). It differs in being petaliferous and usually 4-merous throughout, and its ovary is fully inferior (Table 1). These and numerous other traits of Anisophylleaceae are discussed by Matthews and Endress (2004), giving support to its placement in Cucurbitales despite its divergence in floral form from other families of the order.

An alternative interpretation of the perianth of *Lachnociona*, namely that the conspicuous organs are petals and that an inconspicuous calyx is out of sight beneath them, leads to comparison with a different rosoid group, the family Simaroubaceae of order Sapindales. We have selected the Southeast Asian genus *Eurycoma* (Engler 1931, fig. 175; Nootboom 1962, p. 206) for such a comparison (Table 1). In *Eurycoma*, the conspicuously hairy flowers are unisexual, the 5-lobed superior ovary of 5 free carpels bearing 5 erect, connate or connivent styles which are acute, recurved at the tip, and stigmatic ventrally. In fruit, the 5 carpels separate and spread far apart, as occurs also in *Brunellia*. The androecium of pistillate flowers consists of 5 normal-sized stamens with abortive anthers, alternating with 5 scale-like, much modified staminodes. The 5 hairy petals are spreading-erect and have 5 small sepals at their base. Other than stamen number, therefore, and reflexed rather than erect petals, *Lachnociona* would resemble *Eurycoma*—if we hypothesize that a small calyx is hidden below the “petals.” The fossil thus bears an ambiguous relationship to Simaroubaceae, which we cannot resolve with certainty. In phylogenetic analyses, Simaroubaceae, sensu stricto, are placed in the rosoid II clade (Fernando et al. 1996; Gadek et al. 1996; APG II 2003; Stevens 2001 onwards; Soltis et al. 2005; Schönenberger & von Balthazar 2006).

In summary, the case for postulating a relationship of *Lachnociona* to the clade containing Brunelliaceae and Cunoniaceae rests on the similarity of the following critical floral features: unisexuality, 5-merous actinomorphic perianth, apetalous, abundant pubescence, presence of 10 staminodes in the pistillate flower, 5 carpels, a stout gynoeceal column (which may be) comprised of 5 connivent styles, and sharply acute stylar tips implying a ventrally decurrent stigmatic zone. A superior ovary or ovaries, if present, would be consistent with these families, but if the ovary is interpreted as half-inferior, a similarity would exist to *Pullea* and a few other Cunoniaceae (*Bauera*, f. Dickison, 1975; *Ceratopetalum*, f. Engler, 1930b; *Codia*, f. Hufford & Dickison, 1992) as well as to *Aphanopetalum* and the completely epigynous *Anisophyllea*. A decurrent “sutural” stigma is characteristic of *Brunellia* (Kubitzki 2004) and *Vesselowskyia* of Cunoniaceae (Dickison 1989; Hufford & Dickison 1992).

Our suggestion of a connection with Brunelliaceae and Cunoniaceae cannot be proven, given the difficulty in observing certain critical features of the gynoeceum of *Lachnociona*. However, we believe that the totality of floral features favors placement of the fossil in the rosoid clade of eudicots (e.g., Fernando et al. 1995; Soltis & Soltis 2004; Soltis et al. 2005; Schönenberger & von Balthazar 2006). Except for Saxifragales, the four orders from which we have selected comparative examples are in this large group of angiosperms. According to Friis et al. (2006, p. 7), “(t)he presence of distinctive tricolpate pollen grains in Late Barremian–Early Aptian strata (about 120 Myr) shows that eudicot angiosperms were established in geographically widespread regions early in the history of angiosperms.” Estimates for the ages of crown and stem groups of basal eudicots were presented by Anderson et al. (2005) using *rbcL* sequences and multiple fossil reference points. Their inferred stem and crown group ages for rosoids are 112 mybp and 108 mybp, respectively, and for Saxifragales, the figures are 108 mybp and 102 mybp. In a different analysis, Crepet et al. (2004) dated the minimum age of the “rosoid I” clade as 94+ mybp. Both these estimates are younger than that of Wilkström et al. (2001), which dates the stem group of the rosoids at 125 mybp. As pointed out by Friis et al. (2006, p. 31), “(a) rapid diversification of eudicots, with the emergence of all lineages of basal eudicots before the end of the Albian, has...been inferred, using molecular dating methods.” In this context, the eudicot flowers that have recently been described from Burmese amber of the Late Albian (Poinar 2004; Poinar & Chambers 2005; Poinar et al. 2007), together with the present report, may help open a window to particular features of floral evolution in this period of eudicot diversification.

The flower described here may have been insect-pollinated, as proposed earlier by Santiago-Blay et al. (2005), and it could have been visited by *Melittosphex burmensis*, a small bee recently described from these deposits (Poinar & Danforth 2006). The flower also shows evidence of herbivory, as there is obvious damage to the filaments and anthers by chewing insects.

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